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Behavioral, Ecological, and Evolutionary Aspects of Meat-Eating by Sumatran Orangutans (*Pongo abelii*)

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Abstract Meat-eating is an important aspect of human evolution, but how meat became a substantial component of the human diet is still poorly understood. Meat-eating in our closest relatives, the great apes, may provide insight into the emergence of this trait, but most existing data are for chimpanzees. We report 3 rare cases of meat-eating of slow lorises, *Nycticebus coucang*, by 1 Sumatran orangutan mother–infant dyad in Ketambe, Indonesia, to examine how orangutans find slow lorises and share meat. We combine these 3 cases with 2 previous ones to test the hypothesis that slow loris captures by orangutans are seasonal and dependent on fruit availability. We also provide the first (to our knowledge) quantitative data and high-definition video recordings of meat chewing rates by great apes, which we use to estimate the minimum time necessary for a female *Australopithecus africanus* to reach its daily energy requirements when feeding partially on raw meat. Captures seemed to be opportunistic but orangutans may have used olfactory cues to detect the prey. The

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mother often rejected meat sharing requests and only the infant initiated meat sharing. Slow loris captures occurred only during low ripe fruit availability, suggesting that meat may represent a filler fallback food for orangutans. Orangutans ate meat more than twice as slowly as chimpanzees (*Pan troglodytes*), suggesting that group living may function as a meat intake accelerator in hominoids. Using orangutan data as a model, time spent chewing per day would not require an excessive amount of time for our social ancestors (australopithecines and hominids), as long as meat represented no more than a quarter of their diet.

Keywords Chewing rates · Evolution · Meat-eating · *Pongo abelii* · Seasonality

Introduction

It is generally assumed that in early humans, a calorie-rich, meat-based diet became available through an evolving kit of hunting tools and techniques (Richards 2002). However, Wrangham and colleagues suggest that the shift to a meat-based diet in the human lineage may have been impossible without the knowledge of cooking (Wrangham 2009; Wrangham and Carmody 2010; Wrangham and Conklin-Brittain 2003). Using chimpanzees as a model, Wrangham and Conklin-Brittain (2003) calculated that an early hominin with daily energy requirements of ≤2487 kcal/d (Aiello and Key 2002) would have had to spend 50% of a 12-h day chewing raw meat. This is a significant period for chewing per day because individuals must engage in other activities, and Wrangham and Conklin-Brittain (2003) used these results to support the hypothesis that early humans must have had a technique to tenderize meat, i.e., cooking, for meat to become an important part of their diet.

At present, humans consume an average of 40 kg of meat per capita per year, with several countries reaching >100 kg of meat per capita per year (FAOSTAT 2011). Indeed, humans may rely entirely on meat in certain times of the year, e.g., Iglulik Central Eskimos in winter (Sinclair 1953). Vertebrate meat-eating is also practiced by a number of nonhuman primates such as capuchins (*Cebus* sp.: Rose 1997) and baboons (*Papio anubis*: Strum 1983), in which males typically capture the prey (Rose 1997; Stanford 1999; Strum 1983; Uehara 1997; Wrangham and van Zinnicq Bergmann Riss 1990). In great apes, meat-eating occurs in chimpanzees (*Pan troglodytes*: Boesch and Boesch 1989), bonobos (*Pan paniscus*: Hohmann and Fruth 2008), and Sumatran orangutans (*Pongo abelii*: Utami and Van Hooff 1997). However, in contrast to the diets of humans, those of great apes are composed primarily of fruits and other plant foods. Currently, evidence concerning the social and ecological conditions favoring meat-eating in great apes is scant, with the exception of data for chimpanzees (Gilby and Wrangham 2007; Gilby *et al.* 2006, 2010; Mitani and Watts 2005; Watts and Mitani 2002). For chimpanzees, researchers have proposed 5 hypotheses: the fallback food hypothesis (nutrient shortfall hypothesis), meat-for-sex hypothesis, the nutrient surplus hypothesis, male social bonding hypothesis, and increased visibility hypothesis. There is no evidence to support the fallback food hypothesis, under which meat-eating is predicted to occur during periods of food scarcity (Gilby *et al.* 2006). Hunting frequency was highest during the dry season (Stanford *et al.* 1994b), but it was unclear if food scarcity caused this trend (Gilby *et* *al.* 2006). Equally, there is no evidence for the meat-for-sex hypothesis, whereby meat is exchanged for matings (Gilby 2006; Gilby *et al.* 2006, 2010). However, there is some evidence in favor of the nutrient surplus hypothesis, wherein hunts are more frequent when energy reserves are high (Gilby *et al.* 2006). At least 3 studies have shown that chimpanzees hunt more when ripe fruit is abundant (Gilby and Wrangham 2007; Gilby *et al.* 2006; Mitani and Watts 2005). At Gombe (Gilby *et al.* 2006) and Ngogo (Mitani and Watts 2005), this pattern is the result of increased group size when fruit is abundant, supporting the male bonding hypothesis (Hosaka *et al.* 2001; Mitani and Watts 2001; Stanford *et al.* 1994a), whereas at Kanyawara, the positive effect of fruit abundance on hunting probability remains even after group size is controlled (Gilby and Wrangham 2007). Another ecological factor that has been found to influence meat-eating in chimpanzees is increased visibility. Chimpanzees hunt more in woodland and semideciduous forest vs. evergreen forest (Gilby *et al.* 2006), and in areas where canopy is broken or with secondary growth (Watts and Mitani 2002).

Researchers have observed several cases of meat-eating in wild Sumatran orangutans, although not in Bornean orangutans (*Pongo pygmeus*: Russon *et al.* 2009). However, meat-eating is rare at the Sumatran orangutan sites where this behavior has been observed despite numerous observation hours (van Schaik *et al.* 2003). The available data suggest that unlike other primate species, orangutans do not show a male bias in meat-eating (van Schaik *et al.* 2009). However, a male bias may also be absent in chimpanzees for more opportunistic prey, such as bushbabies (species not reported; Pruetz and Bertolani 2007) and bushbuck fawns (*Tragelaphus scriptus*: I. C. Gilby, *pers. comm.*). Slow loris hunting has previously been observed in 2 adult female orangutans in the Ketambe population (Fig. 1; Utami and Van Hooff 1997), and in 3 individuals (2 adult females and 1 flanged male) at Suaq Balimbing (van Schaik *et al.* 2009). These studies reported a total of 9 cases of orangutans eating slow lorises (Utami and Van Hooff 1997; van Schaik *et al.* 2009). A further case of an orangutan eating a gibbon (Sugardjito and Nurhuda 1981) is also likely to have in fact involved a slow loris (Rijksen and Meijaard 1999). Recently, we observed 3 new

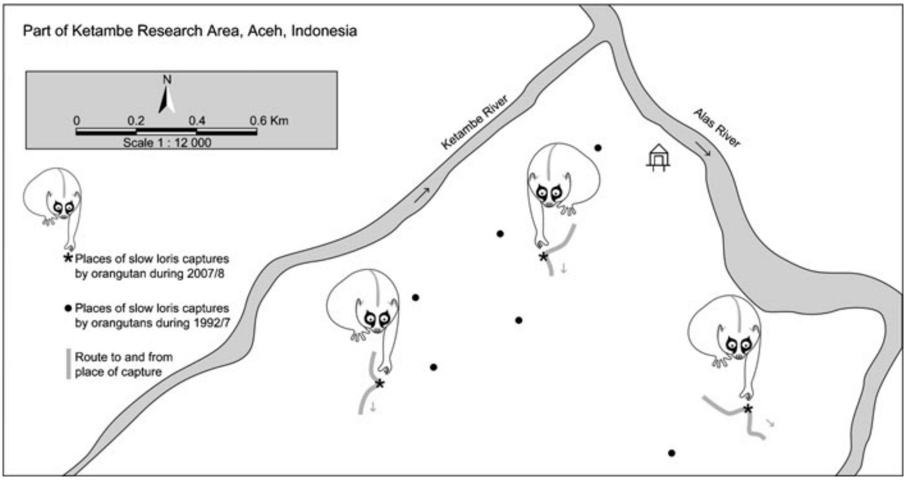


Fig. 1 Slow loris capture locations in the research area of Ketambe, including cases described by Utami and van Hooff (1997). (Illustrations by A. R. Lameira).

cases of meat-eating and recorded details of the meat-eating from prey discovery until the end of prey consumption, including, to our knowledge, the first video recording of the behavior (see supplementary video file). We present these data, complemented with those of previous orangutan meat-eating observations where relevant data are available, and use these data to examine how orangutans find slow lorises and share meat. We also examine when and why orangutans eat meat in light of the hypotheses proposed to explain meat-eating in chimpanzees.

The hypothesis of increased visibility is not applicable to orangutans because they inhabit tropical rain forest with continuous dense canopy throughout dry and wet seasons. However, seasonal variations in high-quality foods may elicit meat hunting. Because previous cases were not reported during mast years (Utami and Van Hooff 1997), this may suggest that the seasonal shortage of food elicits a need for fallback foods in the form of meat (Boesch and Boesch-Achermann 2000; Mitani and Watts 2005; Rose 1997, 2001; Stanford 1996; Teleki 1973). Accordingly, we test whether meat-eating negatively correlates with fruit availability.

Finally, we calculate meat chewing rates, and grams and calories consumed per hour for orangutans and use these to estimate the minimum time necessary for a female *Australopithecus africanus* to reach its daily energy requirements when feeding partially on raw meat. Orangutans have more robust jaws than early humans and are more similar in their dentition to australopithecines than to *Homo erectus* (Grine and Kay 1988). Some australopithecines are suggested to have relied on fruits, and their fallback food may have been harder, tougher (or granular) than fruit (Teaford *et al.* 2002). As this is also the case for orangutans in comparison with chimpanzees (Vogel *et al.* 2008), whose dentition is more similar to that of *Homo erectus* (Wood 1995), orangutans are a useful model in this context.

Methods

We conducted this study at the Ketambe Research Station, Gunung Leuser National Park, Leuser Ecosytem, Sumatra, Indonesia (3°41′N, 97°39′E) between November 2006 and October 2008. The Ketambe research area consists mainly of primary rain forest (Rijksen 1978; van Schaik and Mirmanto 1985) and selectively logged forest. All 3 recent cases involved 1 adult female orangutan (Yet) and her dependent female offspring (Yeni, born in 2001) and occurred in February and December 2007 and in April 2008 (Table I). We refer to Yeni as an infant because she was not yet fully weaned at the age of 6–7 years (van Noordwijk and van Schaik 2005; Wich *et al.* 2004). She was the only individual accompanying her mother during the observed cases of slow loris hunting.

M. E. Hardus, A. Zulfa, and experienced local field assistants observed these new cases during focal follow days, i.e., observations on an orangutan individual, whenever possible from morning nest until evening nest. We collected standardized observational data during each follow day (van Schaik 1999; www.aim.unizh.ch/orangutannetwork.html), comprising feeding time, food species and items, feeding technique, and social interactions between mother–infant and other orangutans. In addition, we drew orangutans' travel path on GPS-constructed maps of the research area, noting the location of each feeding bout. M. E. Hardus collected meat chewing rates during the

Table I Slow loris captures by Sumatran orangutans at Ketambe research station

#	Year	Month	Data available	Reference
1	1989–1991	—	Location	Utami and van Hooff (1997)
2	1989–1991	—	Location	Utami and van Hooff (1997)
3	1989–1991	—	Location	Utami and van Hooff (1997)
4	1992	February	Location, food availability	Utami and van Hooff (1997)
5	1993	April	Location, food availability	Utami and van Hooff (1997)
6	1994	February	Location, food availability	Utami and van Hooff (1997)
7	2007	February	Location, food availability, duration, feeding rate, meat sharing	This study
8	2007	December	Location, food availability, duration, feeding rate, meat sharing, chewing rates	This study
9	2008	April	Location, food availability, duration, feeding rate	This study

slow loris case of December 2007, and insect and leaf chewing rates between April 2007 and January 2008 via video recordings using a Sony HDV 1080i camera with a Manfrotto monopod.

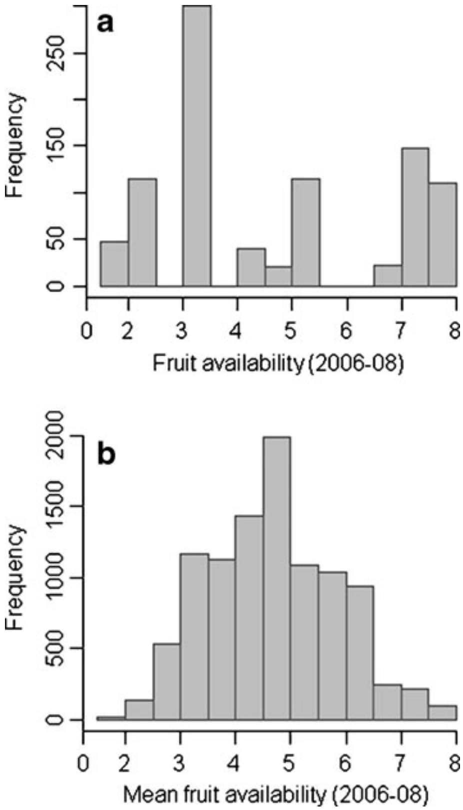
We define food sharing as a transfer of a food item from one individual to another (Feistner and McGrew 1989). We define active sharing as the mother giving food to her begging infant instead of allowing it to take the food (passively tolerant), and active resistance as the mother not letting go of a food item, taking the food out of her infant's hand, or turning her back toward her infant (de Waal 1989; Jaeggi *et al.* 2008).

Experienced assistants recorded fruit availability data monthly from phenology plots (van Schaik 1986; Wich and van Schaik 2000). During 1993–1994, we standardized data on fruit availability by computing *z*-scores due to differences in methods and observers (Wich and van Schaik 2000). During 2006–2008 we calculated fruit availability as the percentage of trees carrying fruits or ripe fruits. We treated these 2 observation periods separately because of these differences.

We developed a Monte Carlo test procedure, written in R version 2.13.0 (R_Development_Core_Team, 2011), to test the null hypothesis that slow loris eating occurred independently of fruit availability (or ripe fruit availability). We explain this method here using the data set collected from November 2006 to September 2008. In this period researchers observed the orangutan mother and infant for 916 follow hours, during which 3 cases of slow loris eating occurred. First, we constructed a frequency histogram showing the distribution of number of follow hours for the different observed fruit availabilities (Fig. 2a). Next, we randomly drew 3 observations of fruit availability according to this frequency distribution, and calculated the mean of these 3 randomly chosen fruit availabilities. We repeated this random drawing of sets of 3 observed fruit availabilities 10,000 times, yielding a null frequency distribution of average fruit availabilities (Fig. 2b). Next, we calculated the observed average percentage of fruit availability at the time of slow loris eating $(2.38+2.13+5.14)/5 = 3.22$, and compared this against the null distribution.

We calculated the left-tailed significance level (P_l) of the observed mean value of 3.22 under the null hypothesis that the slow loris eating occurred independently of the

Fig. 2 (**a**) Frequency histogram showing the distribution of number of follow hours of Yet for the various observed fruit availabilities in 2006–2008. **(b)** Frequency histogram showing the null distribution of mean values of fruit availability for 10,000 sets of 3 randomly drawn fruit availabilities based on the distribution shown in **a**.



fruit availability in the following way. For each of the 10,000 Monte Carlo replications, we compared the observed value 3.22 to the random value. If the random value was less than or equal to, i.e., LTEQ, the observed value 3.22, we increased a LTEQ counter by 1. We then calculated P_l as (LTEQ+1)/(10000+1). (The +1 in the numerator and denominator is to ensure that P_l is greater than 0.) Because we look only at the left-tailed probability we set the critical probability level at 0.025.

We used the same Monte Carlo test procedure to test whether slow loris meat-eating occurred independently of the availability of ripe fruit. We used data from January 1993–December 1994 (period A; Fig. 3a), in which we observed 2 cases of slow loris eating; and for November 2006–September 2008 (period B; Fig. 3b), in which we observed 3 cases of slow loris eating. For period A we calculated the random mean values from 2 randomly drawn observed fruit availabilities, while for period B we based these random mean values on 3 randomly drawn observed fruit availabilities. Unfortunately, observers did not record the number of follow hours from June 1991 to December 1992, so we could not use data collected during this period, although we observed 1 case of slow loris eating in February 1992.

Finally, we performed a Monte Carlo test in which we combined periods A and B. Because researchers used different methods for assessing fruit availability in the 2 periods, we could not combine the data for the 5 cases of slow loris eating that occurred during this whole period. Instead, we performed the Monte Carlo test for

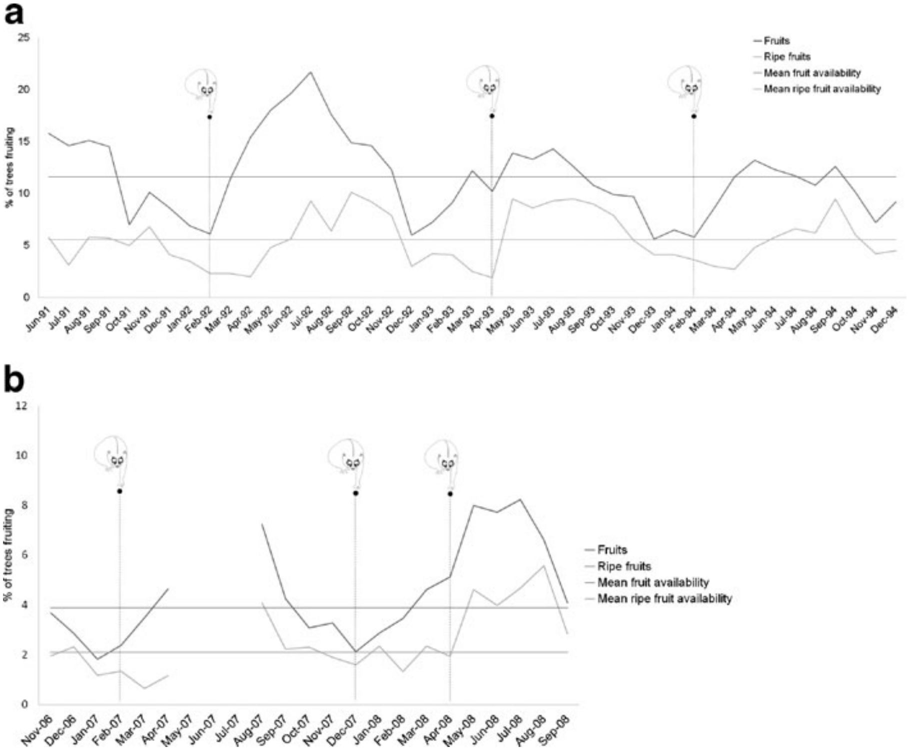


Fig. 3 **(a)** Fruit availability 1991–1994, fruit range (5.6–19.6%), ripe fruit range (1.9–10.1%). The slow loris symbol represents the date of slow loris captures by orangutans. **(b)** Fruit availability 2006–2008, fruit range (1.8–8.0%), ripe fruit range (0.7–4.6%). No data are available for April–August 2007 because of local political unrest. The slow loris symbol represents the date of slow loris captures by orangutans.

both periods simultaneously and calculated a combined left-tailed significance level (P_{l}) in the following way: For each of the 10,000 Monte Carlo replications, we compared the observed value of 8.00 in period A to the random value for period A and simultaneously compared the observed value of 3.22 in period B to the random value for period B. If the random value in period A was less than or equal to the observed value 8.00 *and* the random value in period B was also less than or equal to the observed value of 3.22, we increased a LTEQAB counter by 1. P_{l} was then equal to (LTEQAB+1)/(10,000+1). For instance, if $P_{\mathrm{l}}=0.01$, then the chance of observing a mean fruit availability of 8.00 or less in period A and also observing a mean fruit availability of 3.22 or less in period B, under the null hypothesis that these 2 and 3 fruit availabilities are randomly distributed, was 1%.

Results

Behavioral Data

All 9 observed cases of slow loris-eating at Ketambe occurred at different locations (Fig. 1). In the 3 recent cases of slow loris eating by adult female Yet and her female infant Yeni (Table I), Yet seems to have diverted her travel path along her day route (*ca.* 40 m) to the location where the capture eventually took place, returning to the prior route after consumption (Fig. 1). In each case, Yet turned abruptly (*ca.* 45°, Fig. 1) toward the capture location about 5 min, i.e., 40 m, before capture. After consumption of the loris she turned back sharply, i.e., *ca.* 90° (Fig. 1), and made another 45° turn to continue her previous direction. There was no social event, i.e., the beginning or end of a party or a long call from a flanged male from a distance, at any of the 3 change-points in her route, i.e., before capture, after consumption, and continuation of her prior direction.

Capture started when the orangutan slapped the slow loris, which fell out of the tree, and finished on the ground when the orangutan caught the slow loris and killed it by biting the skull. The consumption process comprised the steps described by Utami and van Hooff (1997), i.e., the female consumed the head, then the genitals, organs, limbs, and other parts of the slow loris; however, in all 3 recent cases, the female ate the limbs immediately after the head. Data on total consumption time were available for the 3 recent cases of meat-eating (Tables I and II).

Although meat sharing took place between the mother and infant, it occurred only when the mother was passively tolerant. Active giving by the mother did not occur. During the first recent case (February 2007), the infant made no attempt to eat the slow loris during the first 12 min after capture. Food sharing then occurred 11 times, including mouth-to-mouth feeding 3 times. Active resistance to food sharing by the mother occurred 3 times but only after 70 min of consumption. During the second case the infant made no attempt to eat from the slow loris during the first 20 min. During this case, hand-to-hand meat sharing occurred 34 times, mouth-to-mouth or mouth-to-hand occurred 5 times, and all 39 occurrences of food-sharing were initiated by the infant. Active resistance from the mother occurred 12 times during the first 2 h of eating. No data on meat sharing are available for the third case (Table I), but the infant ate part of the slow loris some minutes after her mother started to eat.

During the second case the mother had a mean bout duration (seconds) of 27.1± SD 17.4, and a mean number of chews/bout of 24.5±SD 15.6 (N_{bout}=22, N_{chews}= 538), the infant had a mean bout duration (seconds) of 16.3±SD 16 and a mean number of chews/bout of 18.5±SD 13.4 (N_{bout}=6, N_{chews}=98). The mean chewing rate throughout consumption of the mother was 0.95±SD 0.25 chews/s, with a

Table II Feeding time and rates on slow lorises by the focal mother and infant during the 3 recent cases

Year	Month	Time (min) mother	Time (min) infant	Total time	Feeding rate mother (g/h)	Feeding rate infant (g/h)
2007	February	174	114	174	160.9	142.4
2007	December	244	46	244	155.3	137.5
2008	April	140	196	196	141.2	124.8

Time (min) mother and time (min) infant=the feeding time for the adult orangutan female and her infant. Total time=total observation time from moment of capture until end of consumption, during which mother and infant ate the slow loris either alone or together.

maximum of 1.17 chews/s, whereas that of the infant was 0.84±SD 0.29 chews/s, with a maximum of 1.09 chews/s. Chewing rate decreased with time for both the mother (Spearman's ρ: $r=-0.625$, $N=22$, $p=0.002$) and the infant (Spearman's ρ: $r=-0.899$, $N=6$, $p=0.015$). We were not able to determine the exact body parts being eaten at each moment and therefore it was difficult to assess how body part affected the chewing rates. The mean chewing rate for meat was lower than mean chewing rates for insects (1.32±SD 0.19 chews/s, $N_{\text{bout}}=10$) and mature leaves (1.17±SD 0.02 chews/s, $N_{\text{bout}}=8$) by the same mother (Kruskall Wallis: $\chi^2=20.108$, df=2, $p<0.001$; followed by a multiple comparisons *post hoc* test: $p<0.001$ between meat and insects, and meat and leaves).

After consumption of the carcass only a few pieces of bare skin remained, suggesting that the orangutans consumed all of their prey. The mother ate for 244 min at 0.95 chew/s, whereas the infant ate for 46 min at 0.84 chew/s, i.e., the mother ate 1.13 times faster than her infant, meaning that they ate 85.7% and 14.3% of the total slow loris, respectively. Because all 3 cases concern the same type of meat eaten by the same individuals under the same social conditions, i.e., without any other individuals present, we assume that the chewing rates of the first and third case were similar to those of the second case. Using the mean chewing rate for the second case, the mother ate 63.3% and the infant ate 36.7% of the slow loris during the first case, and the mother ate 44.7% and the infant 55.3% during the third case. We assumed via visual assessment of the video recordings that the orangutan ate an adult male slow loris, which has a mass of 737 g (Nekaris and Bearder 2007). Thus, across the 3 cases, this represents a maximum mean feeding rate of 160.9 g/h for an entire adult male slow loris by the adult orangutan and 142.4 g/h by the infant (Table II). If we assume that a slow loris has the same nutritional content as a squirrel, rabbit, or red colobus monkey, 115 kcal/100 g (USDA Food Composition Database; Wrangham and Conklin-Brittain 2003), then the adult female orangutan ingested 185 kcal/h and the infant ingested 163.8 kcal/h.

Ecological Data

Orangutans captured 5 slow loris captures in February and April and 1 in December (no dates were available for 3 cases; Table I). The graphical representation of slow loris captures against (ripe) fruit availability (Fig. 3a,b) suggests that orangutans may be eating slow lorises particularly during periods of low (ripe) fruit availability.

For period A the observed mean fruit availability at the time of slow loris eating is (10.2%+5.8%)/5=8.00%. The P_1 of observing ≤8.00 is 0.14. The observed mean ripe fruit availability at the time of slow loris eating is (1.9+3.6)/2 =2.75 (P_1=0.08). For period B, the observed mean fruit availability at the time of slow loris eating is (2.38+ 2.13+5.14)/3 =3.22% (P_1=0.11) (Fig. 2). The observed mean *ripe* fruit availability at the time of slow loris eating is (1.34+1.60+1.95)/3 =1.63% (P_1=0.23). Combining the two periods, the P_1 of observing a mean fruit availability of ≤8.00 in period A and ≤3.22 in period B is 0.016. The P_1 of observing a mean ripe fruit availability of ≤2.75 in period A and ≤1.63 in period B is 0.017. These results show that slow loris eating by orangutans occurred significantly more often in periods of low fruit availability and low ripe fruit availability.

Discussion

Meat-eating in orangutans is a rare event, which makes it difficult to examine. Owing to the small sample size in this study, any generalizations should be treated with caution.

How Do Orangutans Find Slow Lorises?

All known cases of slow loris capture and eating at Ketambe, including the 3 most recent observations, occurred at locations scattered through the area (Fig. 1). Hence, encounter and predation of slow lorises by orangutans most likely occurred opportunistically because the events were not related to any particular locations (Utami and Van Hooff 1997). This is also often the case in other instances of predation by primates (Stanford 1998). Nevertheless, the 3 recent cases indicate that the adult female diverted her travel path to the location where the capture took place, returning to the previous route after consumption. Identifying potential travel goals is a major exercise in itself (Byrne *et al.* 2009). However, we tentatively interpret the orangutan's deviation in her travel route in biological terms, suggesting that she had the goal of capturing a slow loris, for 3 reasons. First, if the turn was not the effect of a decision-making process, we would expect either straight-line or random travel. However, Yet turned abruptly (±45°, Fig. 1) toward the capture location *ca.* 5 min, i.e., 40 m, before the actual capture, suggesting that she did not anticipate a remembered site and traveled toward it in a straight line, nor was she traveling randomly and unexpectedly encountered a slow loris in her path. Moreover, Yet turned sharply back to her previous route after consumption, supporting the view that there was a meaningful cause for her previous deviation. Second, no social events coincided with the change points in her route. Third, the pattern in her travel route is consistent across the 3 recent cases (Fig. 1) and does not coincide with the approach to other important food sources at Ketambe, such as fig trees (Wich, Hardus, and Lameira *pers. obs.*). New methods, e.g., change-point test (Byrne *et al.* 2009) for objectively determining an animal's travel path could be used to elucidate this matter in the future (Asensio *et al.* 2011).

Slow lorises are solitary nocturnal strepsirrhines, meaning that they are difficult to locate for a diurnal primate, such as orangutans (Bearder 1987). Slow lorises live in the main canopy, prefer the forest edge (Johns 1986), and sleep in sites such as tree holes and crevices (Choudhury 1992). If we accept that the orangutan changed her course toward the capture location purposely, then, although it is possible that the orangutan observed the slow loris from a distance, she may also have been able to identify a potential sleeping location or microhabitat, e.g., trees with particularly dense epiphytes. Alternatively, the orangutan could have used olfactory cues to find a slow loris. Lorises use olfactory communication (Charles-Dominique 1977; Nekaris and Bearder 2007), and a trained observer can smell a loris ≤50 m away (Alterman 1995); thus, plausibly, slow loris olfactory communication may have also been intercepted by the orangutan. Future experiments should test this hypothesis.

Similar to that in most primate species (Brown *et al.* 2004), meat sharing in orangutans occurred only between mother and infant, although in chimpanzees and bonobos it has also been observed between wild adult males and females (Rose 1997; Stanford 1999). No other adult orangutans were in the vicinity of our observed cases, so it remains to be determined whether the lack of meat sharing between adult orangutans is simply a consequence of semisolitary living. Our results show that the infant initiated all meat sharing. This is similar to transfers of other foods between mother and infant orangutans (Jaeggi *et al.* 2008) and with food transfers in other mother–infant primates (Nishida and Turner 1996; Rapaport and Ruiz-Miranda 2002; Ueno and Matsuzawa 2004).

When and Why Does an Orangutan Eat Meat?

Because orangutans did not travel in parties while capturing a slow loris and did not share their meat with unrelated individuals, the meat for sex hypothesis (Mitani and Watts 2005; Stanford *et al.* 1994a; Teleki 1973) and the male social bonding hypothesis (Mitani and Watts 2001, 2005; Mitani *et al.* 2002; Takahata *et al.* 1984), are not applicable. However, we found that slow loris eating by an orangutan occurs significantly more often in periods of low fruit and low ripe fruit availability. Thus, the orangutan preyed on slow lorises during periods of food scarcity. We were unable to include data for the 1 case of slow loris eating in February 1992 in this test. However, this case occurred during a month with extremely low fruit availability and low ripe fruit availability, meaning that it is very likely that if including these data would strengthen our conclusion that slow loris eating occurs particularly in periods of low (ripe) fruit availability.

Several ecological factors and prey characteristics may affect seasonality of meat-eating in primates. Because orangutans and slow lorises both feed on fruits (slow lorises are only slightly less frugivorous than orangutans, Nekaris and Bearder 2007), encounters followed by capture of lorises should increase in frequency when both species are attracted to common resources (Stanford 1998). However, this is unlikely because orangutans are diurnal primates, whereas slow lorises are nocturnal and their sleeping sites are far from the nearest feeding site (K. A. I. Nekaris *pers. comm.*).

Captures are also expected during the prey's birth period (Boesch and Boesch-Achermann 2000; Fedigan 1990; Mitani and Watts 2005; Rose 1997, 2001; Takahata *et al.* 1984). However, orangutans have never been observed to eat young lorisines, making this explanation for the timing of slow loris capture improbable. Orangutans may simply capture slow lorises during food scarcity because they spend more time traveling in search of food, and thus are more likely to encounter a slow loris by chance. This, however, is unlikely, because orangutans reduce travel and feeding time and increase resting time during food scarcity (Knott 1998; Wartmann *et al.* 2010). Moreover, other differences in range may not be sufficient to explain the occurrence of slow loris hunting because males have wider ranges than females (Singleton and van Schaik 2001), but slow loris hunting is not biased toward males (van Schaik *et al.* 2009), and because not all females of the same population, which experience the same periods of food scarcity, show this behavior.

Human observers are often oblivious to the presence of slow lorises in the forest, and to the best of our knowledge they have not been observed during orangutan follows except when one is actually hunted by an orangutan. It is therefore difficult to provide a measure of encounter rate of slow lorises and to test whether orangutans target slow lorises during food scarcity. However, this may be assessed indirectly by examining an alternative hypothesis: that orangutans encounter slow lorises while foraging for dispersed food, such as insects, during food scarcity (van Schaik *et al.*

2009). According to this hypothesis, time spent feeding on insects should negatively correlate with fruit availability. However, we found no correlation between fruit availability and time spent feeding on insects by the female orangutan (Pearson correlation for 2007–2008: $N=11$, $r=-0.481$, $p=0.134$). Moreover, during the 2 periods (1991–1994 and 2007–2008), the maximum time spent feeding on insects recorded for this female was 25.8% (June 1993), but slow loris captures occurred when the female spent 12.9% (April 1993), 16.8% (February 2007), 16.7% (December 2007), and 7.4% (April 2008) of her time feeding on insects, indicating that this activity did not necessarily lead to more slow loris encounters. Further, when plotting time spent feeding on insects per month for all females living in the Ketambe area, this particular female (Yet) did not seem to be an outlier vs. other adult females (Fig. 4).

Evidence of orangutan meat-eating supports the fallback food hypothesis, contrary to findings for chimpanzees (Gilby and Wrangham 2008; Gilby *et al.* 2006; *cf.* Pusey *et al.* 2005; Stanford *et al.* 1994a). Marshall and Wrangham (2007) classify 2 fallback foods: staple and filler fallback foods. Staple fallback food serves as the sole food supply when preferred food is scarce and thus is an abundant food that is available year round. Filler fallback foods are rare and usually of high quality (Constantino and Wright 2009; Marshall and Wrangham 2007; Marshall *et al.* 2009). Meat can be considered to be a filler fallback high-quality, energy-rich food for Sumatran orangutans because the availability of preferred fruits is low when meat is eaten (Kaplan *et al.* 2000; Knott 2005; Marshall and Wrangham 2007; Marshall *et al.* 2009; Milton 1999). Although slow loris densities may be highly variable (Wiens and Zitzmann 2003), they are nevertheless considerably less dense than other food sources usually considered as orangutan staple fallback foods, e.g., bark, leaves, figs, and they probably exist in densities more similar to those of other filler fallback foods, such as honey.

The saliva of the slow loris is toxic and is used in defense against predators (Alterman 1995). Thus, orangutans should avoid such a risk when their dietary intake can be derived from available risk-free resources, e.g., ripe fruit. This risk

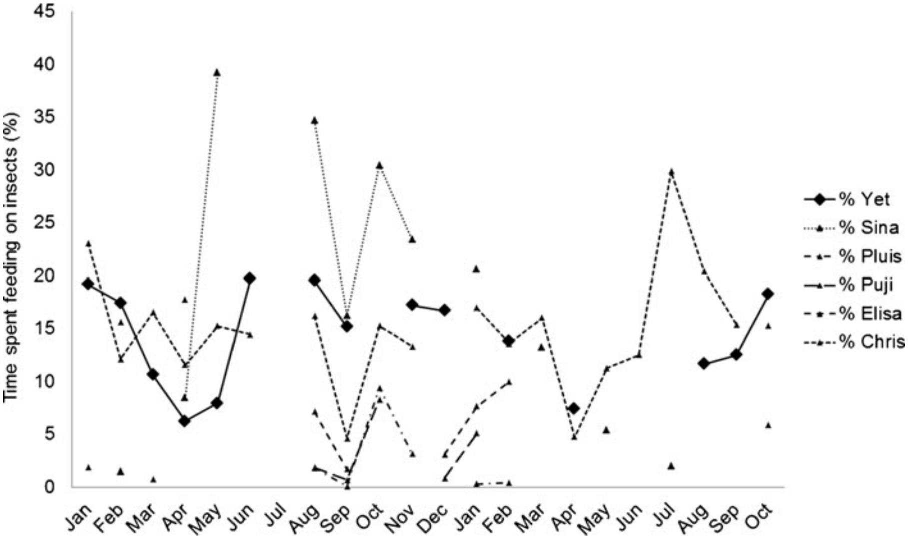


Fig. 4 Time spent feeding on insects per month for 6 adult females in the Ketambe area during 2007 and 2008.

might also explain why wild orangutans slap their slow loris prey out of the tree, to knock the prey unconscious and avoid being bitten, before descending rapidly to the ground to capture and kill the loris with a bite to the head. An unsuccessful attempt at capture on the ground (after slapping) at Suaq Balimbing, Sumatra (A. Permana *pers. comm.*), suggests that orangutans may risk losing such a valuable prey to avoid being bitten.

Slow loris hunting likely represents a cultural behavior (van Schaik *et al.* 2003, 2006) and this may explain why some individuals seem to be specialist slow loris hunters, but other individuals of the same population living in the same area do not show the behavior. Yet, whose capture rate is *ca.* 30 times higher than anyone else's (van Schaik *et al.* 2009), is the most dominant female in Ketambe, a status that may not favor social transmission of the behavior in semisolitary orangutans. Future studies should focus on the family lineages of individuals showing the behavior to address this question.

Chewing and Feeding Rates and Evolutionary Aspects of Meat-Eating

The chewing rate of meat-eating in an adult orangutan was lower than insect and leaf chewing rates. This may be explained by the generally low fat percentage and collagen richness of wild tropical mammal meat, which makes it tough to chew (Lucas and Peters 2000). Unpublished data for other cases of meat-eating by orangutans at Suaq Balimbing also show that individuals chew meat for several hours (C. P. van Schaik *pers. comm.).*

Orangutans used more than twice the amount of time (160.9 g/h) to eat the same amount of meat than chimpanzees (348 g/h) (Wrangham 2009; Wrangham and Conklin-Brittain 2003). Other chimpanzee data shows that this species is able to consume meat at much higher rates, i.e., 1.9±1.2 kg/h (Gilby 2006). This difference between orangutans and chimpanzees may suggest that higher sociality in chimpanzees influences intake rates, where individuals are surrounded by conspecifics when eating meat, and where meat is a highly preferred food item and stealing occurs (Boesch and Boesch 1989; Goodall 1986; Stanford 1999). In chimpanzees, feeding rates on meat are slower when many other individuals are present (Gilby 2006). Although this seems to contradict the sociality hypothesis within species, the minimum values in these cases remains much higher than in orangutans, e.g., more than 500 g/h with 10 beggars (Gilby 2006), supporting the hypothesis.

One of the largest-brained australopithecines, i.e., *Australopithecus africanus* (McHenry 1982) has an estimated energy requirement of 1202–1507 kcal/d (Aiello and Key 2002). According to orangutan data (ingestion rate of 185 kcal/h), *Australopithecus africanus* would have had to chew for *ca.* 2 h to achieve 25% of these caloric requirements purely from meat (Table III, orangutans × *A. africanus*), while achieving the remaining 75% of its caloric requirements from food sources with faster chewing/intake rates, e.g., leaves or insects. This constitutes a considerable period of the day for orangutans, which spend *ca.* 6 h/d feeding (Morrogh-Bernard *et al.* 2009), and does not include the time necessary for the collection of vertebrate prey.

In comparison with semisolitary orangutans, australopithecines are assumed to have lived in social groups (Copeland *et al.* 2011). Therefore, an individual may not have been responsible for procuring all of its own calories, reducing search and hunt

Table III Time chewing on raw meat required to satisfy 25% of an individual's energy daily requirements vs. feeding rates of orangutans and chimpanzees and daily energy requirements of *Australopithecus africanus* and *Homo erectus*

Daily energy requirements Feeding rate	*Australophitecus africanus*: 1507 kcal/d[a]	*Homo erectus*: 2487 kcal/d[b]
Orangutans: 185 kcal/h	2.04 h	3.36 h
Chimpanzees: 400 kcal/h[b]	0.94 h	1.55 h[c]

[a] Aiello and Key (2002).

[b] Wrangham and Conklin-Brittain (2003).

[c] *cf.* Wrangham and Conklin-Brittain (2003).

time. It is also reasonable to assume that biomechanics of the craniodental morphology between orangutans and chimpanzees do not sufficiently explain the differences in feeding rates on raw meat between both species. Therefore, group living as opposed to (semi-)solitary living may have played an important role as an intake accelerator. Higher sociality in australopithecines and *Homo* would have reduced the time needed to chew on meat by increasing feeding rates, as observed in chimpanzees (Table III). Thus, time needed to chew on raw meat would not impede a social early human from consuming a 25% meat-based diet. These findings differ from the results of Wrangham and Conklin-Brittain (2003) in that we use a 25% meat diet in a human ancestor, instead of a 100% meat diet. We set the meat diet at 25% because excessive protein consumption is unhealthy for humans, becoming toxic or lethal when consumed too much by noncarnivores (Speth 1987, 1989; Speth and Spielmann 1983), and causing negative effects on infants, e.g., lower birth weights, when pregnant females surpass 25% protein in their diet (Speth 1989, 1990). This implies that the cooking hypothesis (Wrangham 2009; Wrangham and Conklin-Brittain 2003), as a means to reduce time spent chewing on meat, will be further supported only when it is shown that meat represented more than a quarter of the total diet of our social ancestors.

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